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STUDIES ON FUNCTIONAL MORPHOLOGY IN THE DIGESTIVE SYSTEM OF *OREASTER RETICULATUS* (L.) (ASTEROIDEA)

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JOHN MAXWELL ANDERSON

Division of Biological Sciences, Cornell University, Ithaca, New York 14853

Oreaster reticulatus (Fig. 1) is a large, conspicuous, and easily-recognized sea-star, abundant within its broad geographical range and probably of considerable ecological significance where it occurs. Curiously, however, the number of published papers dealing with aspects of the basic biology of this species is small. A brief note by Thomas (1960) describes its feeding habits; another, almost as brief, by Matthews and Lima-Verde (1968) suggests an ecological relationship between *Oreaster* and two species of *Panulirus* on the fishing-banks of Northeastern Brazil. The entire literature dealing with the internal anatomy of *O. reticulatus* appears to consist of a four-page paper with three plates by Tennent and Keiller (1911) and a brief abstract by Anderson (1967) reporting preliminary observations on the digestive system. Some special features of the internal anatomy of *Calceita*, a genus assigned to the Family Oreasteridae, were described and figured (rather sketchily) by Müller and Troschel (1842), whose drawing was reproduced by such later authors as Ludwig and Hamann (1899); but beyond this, published information on *Oreaster* and its relatives is scanty. The purpose of the present paper is to describe, in greater detail than that provided in previous accounts, the general morphology of the digestive system as a whole, noting particularly some interesting features of the pyloric stomach and related structures. This is intended as a contribution toward a broadly comparative survey of digestive systems among asteroids. Such a survey has never been undertaken; a step in this direction is provided by Anderson (1966), and a further contribution appears in Jangoux and van Impe (1971), but available data are still inadequate to permit comparisons in detail among representatives of many different families of sea-stars. Further, an attempt will be made to draw together published and unpublished descriptions of feeding behavior in *Oreaster*, and to correlate these with structural features of the digestive system. The results of histological studies on this system are to be published in a subsequent paper.

Paraphrasing a statement concerning *Oreaster* that he had published in 1902,

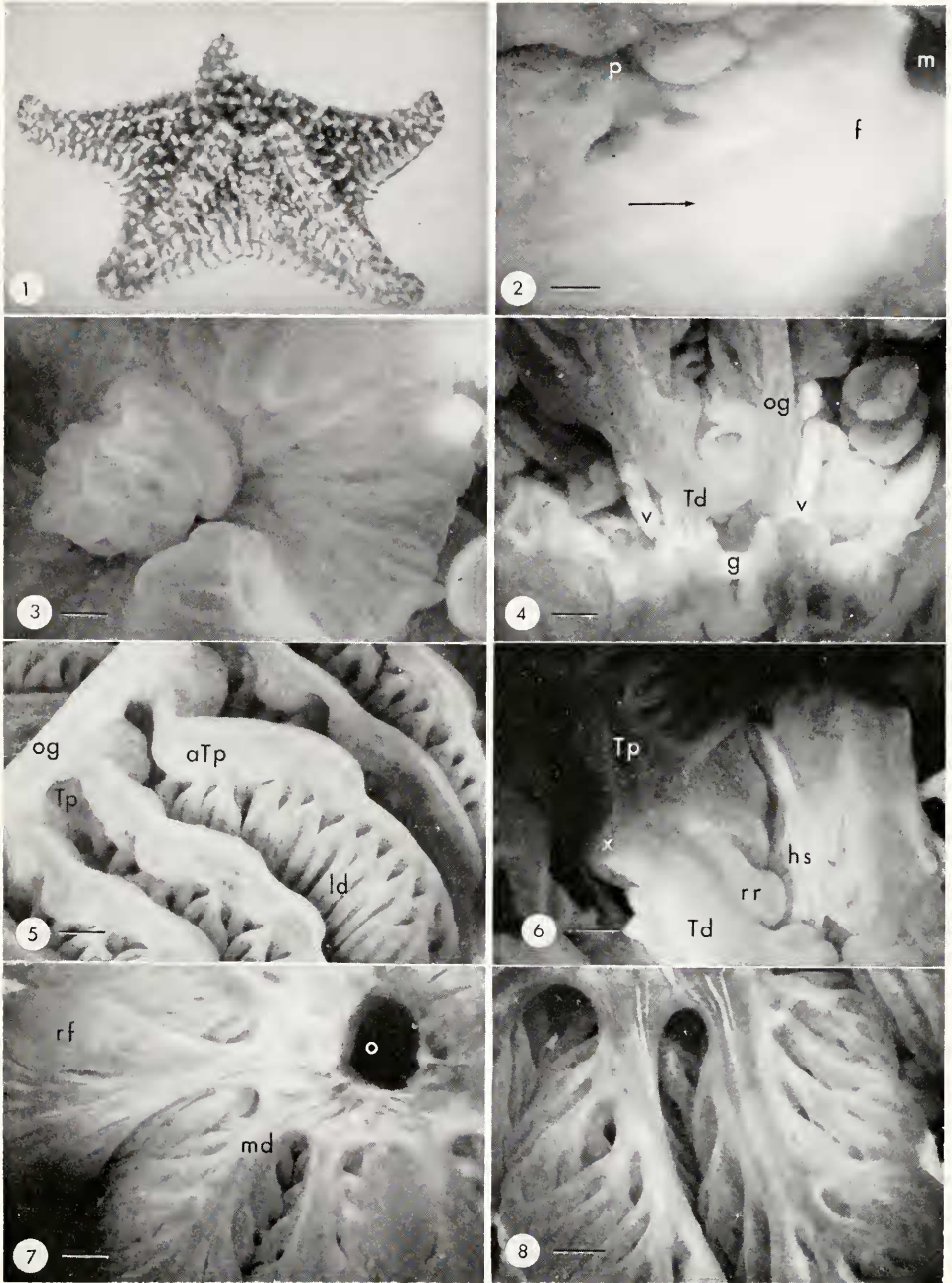


FIGURE 1. *Orcaster reticulatus*. The major radius of this specimen measured about 12 cm (from a color transparency by C. P. Anderson).

FIGURE 2. The floor of the cardiac stomach, internal view. The arrow indicates the dis-

H. L. Clark (1933, p. 22) says: "This is undoubtedly the best known of West Indian sea-stars, since it has been taken to many parts of the world in the past 175 years as a typical curio and souvenir of the region." It is a widely distributed species, being common, according to Downey (1973), in shallow-water grass and sand flats from Florida to Brazil; it occurs in the Cape Verde Islands and in Bermuda, and it is occasionally found as far north as Cape Hatteras. Overall, however, the scientific interest it has attracted is rather limited. A. Agassiz (1877) gives a meticulous and beautifully illustrated description of its skeletal morphology, and the species is, of course, treated in systematic and faunistic studies, such as those cited above, and others (among them Verrill, 1915, and Caso, 1961). Increased attention to other interesting features of this species seems long overdue.

MATERIALS AND METHODS

Specimens were obtained from a commercial source in the Florida Keys. At the laboratory, they were maintained in large aquaria provided with running sea water and were fed periodically with crushed snails, shucked bivalves, and pieces of fish, all of which they ate. Under these conditions they remained in an evidently healthy, vigorous state until sacrificed for study. Animals to be dissected were first soaked until flaccid in a solution of $MgSO_4$ (8% in tap water). The specimens were all rather large, with major radii ranging from 10 to 14 cm. In such animals, as pointed out by Tenment and Keiller (1911), the body wall is exceedingly hard and tough, and gaining access to the internal organs is unusually difficult. The technique eventually adopted was as follows: using a strong, sharp scalpel (with a well-taped handle), a horizontal incision was made around the periphery of

tinct line bounding the smooth, yellowish central area. Abbreviations are: *m*, mouth opening; *f*, floor; and *p*, a lateral pouch.

FIGURE 3. Pouches of the cardiac stomach, partially everted and not fully inflated with coelomic fluid. These show the typical asteroid branching gutter-patterns in the wall, here seen from the mucosal side.

FIGURE 4. Oral view of the origins of a pair of Tiedemann's ducts, and related structures. Abbreviations are: *g*, fibrous girdle, just above remnants of the cut wall of the cardiac stomach; *v*, vertical anchoring strands suspending the girdle from the roof of the disc; *Td*, Tiedemann's duct; and *og*, an oral gutter of Tiedemann's pouch.

FIGURE 5. Detail of a portion of a pyloric caecum, with associated structures, seen from below. Abbreviations are: *og*, oral gutter; *Tp*, striated side wall of the main Tiedemann's pouch; *aTp*, accessory Tiedemann's pouch; and *ld*, lateral diverticulum of a glandular pocket of the pyloric caecum.

FIGURE 6. Oral view of the proximal portions of two radial branches of the pyloric stomach, with related structures. Abbreviations are: *Td*, Tiedemann's duct, transected at *x*; *Tp*, Tiedemann's pouch; *rr*, radial reservoir of the pyloric stomach; and *hs*, horizontal connective-tissue sheet, which joins with the vertical anchoring strands to provide support for the roof of the pyloric stomach.

FIGURE 7. Aboral view of the roof of the pyloric stomach, after removal of the intestine, intestinal caeca, and rectum. Abbreviations are: *o*, opening from the pyloric stomach into the intestine; *rf*, roof folds in one of the paired fold-pattern sets; and *md*, main duct or channel of a fold-pattern, showing supposed hemal vessels in its roof.

FIGURE 8. A closer view, showing structural details of a pair of fold-patterns in the roof of the stomach.

For each figure, the scale bar shown represents 1 mm.

each ray, and the incisions in adjacent rays were joined by cutting through inter-radial structures. When the oral and aboral parts of the body wall were thus separated, the aboral wall was removed by carefully cutting all mesenteries and connective-tissue strands by which the viscera were suspended from it, and by transecting the gut just below the anus. The viscera were then floated up in the relaxing solution, the dissection continued, and the desired observations made. Anatomical details were photographed in freshly dissected, living specimens, using a 35 mm camera mounted on a dissecting microscope.

OBSERVATIONS AND RESULTS

The central cavity of the cardiac stomach has a smooth floor, continuous at the mouth with the external peristomial membrane (Fig. 2). The floor shows fine radial striations or wrinkles, and in all specimens examined it was of a yellowish color, contrasting with the generally brown cast of the rest of the stomach. A distinct boundary-line marks the margin of the floor, and just beyond it are ranged the regularly-spaced oral terminations of a large series of typical branching gutter-patterns in the wall of the stomach (Fig. 3). The wall is folded into a series of pouches, one set for each ray. In the fully retracted condition a set of these pouches lies above the proximal part of the ambulacral ridge pertaining to its radius in the floor of the disc, bounded on either side by an interradial septum. Each set of pouches comprises a thin-roofed median portion and a pair of complexly folded lateral pockets. The lateral pockets or pouches in adjacent rays are joined together by smooth walls, thrown into loose folds and passing around the interradial septa. These smooth walls, with inward extensions from the roofs of the several median pouches, continue upward to the aboral boundary of the cardiac portion of the stomach. This is more or less arbitrarily recognized as a slightly constricted region which in *Oreaster*, as in *Patiria* (Anderson, 1959), is marked by an encircling connective-tissue girdle related to the suspensor-retractor system to be described later.

The overlying pyloric stomach is tall in its oral-aboral dimension and is deeply divided radially in relation to the origins of the paired pyloric caeca to which it gives rise. The radial indentations, alternating with the pyloric caeca and their specialized appendages, are like those described in several other sea-stars. The similar condition found by Jangoux and van Impe (1971) in *Asterina*, *Henricia*, and *Echinaster* leads these authors to state that there is no pyloric stomach in the classical sense, but rather a characteristic structure which they call the "*complexe stomacal supérieure*." For each pyloric caecum a separate duct originates from the stomach, arising just above the level of the girdle (Fig. 4); using the terminology applied to the similar structure in *Henricia* (Anderson, 1960, p. 377), this is referred to as Tiedemann's duct. In its proximal part each duct is a cylindrical tube, the lumen of which is set off by a distinct partition from the space above it. After proceeding a short distance, however, it opens out to form the oral gutter of a deep Tiedemann's pouch, the cavity of which is continuous aborally with the central duct of the pyloric caecum proper. This central, aboral duct (which, it will be understood, has no floor) gives off, alternately to right and left, side branches which are the ducts of a long series of typical glandular pockets, extending all the way to the distal end of the caecum. The side walls of these pockets are thickened

and folded vertically to form lateral diverticula. The most striking and conspicuous feature of these organs is the presence of an accessory or secondary pouch hanging below each lateral glandular pocket, in effect branching from the side walls of the main Tiedemann's pouch. They are provided with oral gutters which originate just above the main gutter, and they taper upward and outward to end a variable distance from the tip of each pocket. The walls of the secondary pouches are faintly marked by narrow, evenly-spaced, parallel vertical striations which give the appearance of separating adjacent channels in the lumen of the pouch. Such markings are present also in the side walls of the main Tiedemann's pouch. All of these features are shown in Figure 5. In all respects, the pyloric caeca and Tiedemann's pouches of *O. reticulatus* resemble very closely the corresponding structures in *Porania pulvillus*, as previously described (Anderson, 1961, 1966).

It was mentioned earlier that the pyloric stomach is deeply indented between the bases of the pyloric caeca. Alternating with the indentations are radiating branches of the stomach, corresponding in position with the Tiedemann's ducts just below them; their side walls taper outward and become continuous with the proximal ends of the main Tiedemann's pouches. Just proximal to the point of origin of the first of the lateral glandular pockets from the central aboral duct, at about the level where the tubular Tiedemann's duct opens to become the oral gutter, a change in the gross appearance of the side walls of the organ occurs. The line marking this change is interpreted as the boundary between Tiedemann's pouch and the radial branch of the pyloric stomach. Aborally, this branch receives the central duct of the pyloric caecum. In position and anatomical relationships (Fig. 6), it corresponds precisely to the structures observed in the digestive systems of *Henricia* and *Linckia* and termed "radial reservoirs" of the pyloric stomach (Anderson, 1960, 1966).

The roof of the pyloric stomach in *Oreaster* presents a specialized feature which has not, to my knowledge, been described in any other sea-star. Tennent and Keiller (1911) write of it as follows (p. 114): "Beneath the intestine, upon the surface of the stomach in each radius, is what appears at first sight to be a second set of five caeca, each made up of two parts. Further examination shows that these are merely pouches formed by the folding of the upper wall of the pyloric portion of the stomach. They involve the regions into which the ducts of the pyloric caeca open and have a narrow slit-like connection with the stomach." Unfortunately, these unique structures, so succinctly characterized, cannot be made out with certainty in Tennent and Keiller's plate showing an aboral view of the digestive system. As seen in Figure 7, the roof of the pyloric stomach has a relatively smooth portion surrounding the opening into the overlying intestine. Radiating from this central area are the five sets of "pouches" just described. This term seems inappropriate; the structures referred to are radially-arranged fold-patterns, like inverted grooves or gutters, in the roof of the pyloric stomach. In each pattern, the folds converge on a major channel leading toward the intestinal opening. Each member of a pair of fold-patterns lies above a radial reservoir, and the cavities of the fold-pattern and the reservoir communicate by way of the "narrow slit-like connections" mentioned by Tennent and Keiller. There are numerous conspicuous vessels, probably parts of the hemal system, running in the aboral walls of the main channels (Figs. 7, 8). Figure 9, a semidiagrammatic cross-section, shows the

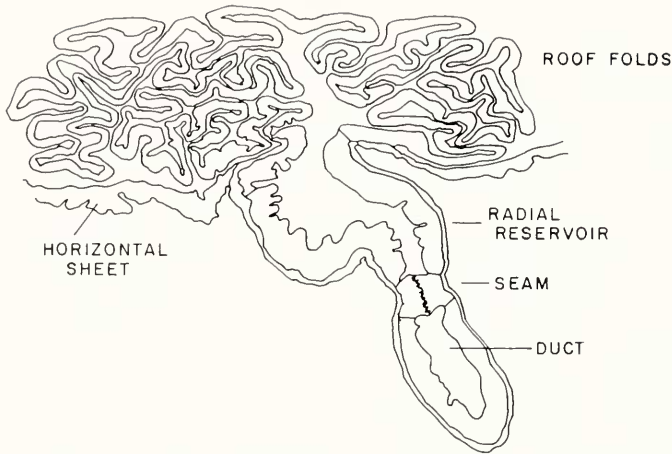


FIGURE 9. Semidiagrammatic cross-section of a radial portion of the pyloric stomach, showing the relationships between its component parts. This section is at a level proximal to the point at which Tiedemann's duct opens out to form the oral gutter of Tiedemann's pouch. The seam forming the partition between the duct and the overlying radial reservoir is maintained by permanent adhesion between cells in opposite walls. The figure was made by tracing, with some reconstruction, a projected histological section.

relationships between the fold-pattern, the radial reservoir, and the Tiedemann's duct pertaining to a single pyloric caecum. The close correspondence in position between the paired sets of fold-patterns and the paired pyloric caeca strongly suggests a significant functional relationship.

The intestine in *Oreaster* is a large, flattened, generally pentagonal organ. From its corners five flat prolongations extend outward in the interradii, crossing the roof of the pyloric stomach between adjacent sets of fold-patterns (Fig. 10). Each extension bifurcates as it reaches the interradiial septum, and the ten branches thus formed become the very large and conspicuous intestinal caeca. The main duct gives off numerous bladder-like diverticula, and the whole organ, according to Tennent and Keiller, is capable of great distention. The intestinal caeca of *Oreaster* are very similar to those of *Culecita*, as illustrated by Müller and Troschel (1842); see also Ludwig and Hamann (1899, p. 585 and Plate IV).

The rectum is short, arising from about the center of the roof of the intestine and passing directly through the aboral body wall. The opening from the intestine into the rectum lies immediately above the passage leading from the pyloric stomach into the intestine (Fig. 11).

The complement of fibrous strands, sheets, and mesenteries developed in *Oreaster* to suspend and secure the digestive organs in the spacious body cavity, and to bring about retraction of the eversible parts, is very complex. Some account of this system will be helpful in understanding functional relationships.

The pyloric caeca are suspended from the aboral body wall by the usual paired, parallel mesenteries, which form continuous narrow sheets and enclose between them a long, tubular coelomic space above the central duct of each caecum. The mesenteries are unusually thick and tough in *Oreaster*, and they send short ex-

tensions laterally to suspend the glandular pockets of the caecum. Proximally, the mesenteries mingle with the fibrous bands by means of which the ducts of the intestinal caeca are hung from the roof of the disc, and become continuous also with a thick horizontal sheet which covers the roof of the pyloric stomach (Fig. 10). The sheet extends between the proximal ducts of the intestinal caeca, and it surrounds and attaches to the lower margins of the paired fold-patterns in the roof of the pyloric stomach. In each of the paired units, the level of attachment to the stomach is the line of transition between fold-pattern and radial reservoir (Figs. 6, 9, 10).

Additional suspension is provided for the digestive system by a pair of bands in each ray which originate on the aboral body wall and pass downward. Each of these vertical bands makes a connection with the mesentery complex at the edge of the horizontal sheet and then continues, passing lateral to a radial reservoir and joining the fibrous girdle encircling the cardiac stomach (Fig. 4). Strong bands, which I have termed "oral anchors," proceed from these junctions on the girdle to firm attachments alongside the proximal ambulacral ossicle in each ray (Figs. 12, 13).

In each radius, a group of glistening white extrinsic retractor strands arises from each side of the proximal end of the ambulacral ridge. From broad origins along the ridge, the fibers converge as they pass upward beside the pouches of the cardiac stomach and form three major branches (Fig. 13). One of these spreads over the roof of the median pouch, attaches to it along a line of insertion running radially, and sends further branches orally in its wall. The second distributes principally to the nearby lateral stomach pouch, where it bifurcates repeatedly (Fig. 14). Its branches, and those of the first major strand, give rise to the downward-coursing intrinsic retractor elements on and in the walls of the stomach, spreading out in patterns corresponding to those of the gutters mentioned earlier. These intrinsic strands are very similar in appearance and distribution to those designated "class 1" fibers in *Patiria* (Anderson, 1959). The third major extrinsic branch sends a few subsidiaries to nearby pouches and then passes directly to the girdle on the cardiac stomach, which it joins near the point of attachment of one of the vertical suspensory bands descending from the roof of the disc. I have designated this branch the "girdle retractor."

It is to be understood that all of the extrinsic retractor elements just described are paired; that is, in each ray there are two sets of the three main retractor branches, which arise and distribute symmetrically on either side of the axis of the ray.

Turning again to the intrinsic retractor strands, it is worth noting that in addition to the class 1 type previously described, other small branches are present. Considerable numbers of short, slender fibers originate on the folds and ridges of the lateral pouches and run horizontally, outside the wall of the stomach, before entering it again (Fig. 15). These strongly resemble the "class 2" fibers of *Patiria*. In the lowest part of the stomach groups of 3 to 12 thin strands emerge from folds related to the terminal gutter-patterns and run vertically, free in the coelom, to insertions on the outer surface of the smooth floor of the cardiac stomach (Figs. 16, 17). They are similar to the "class 3" fibers found in *Patiria* (Anderson, 1969). Precise correspondence between these fiber types cannot be firmly

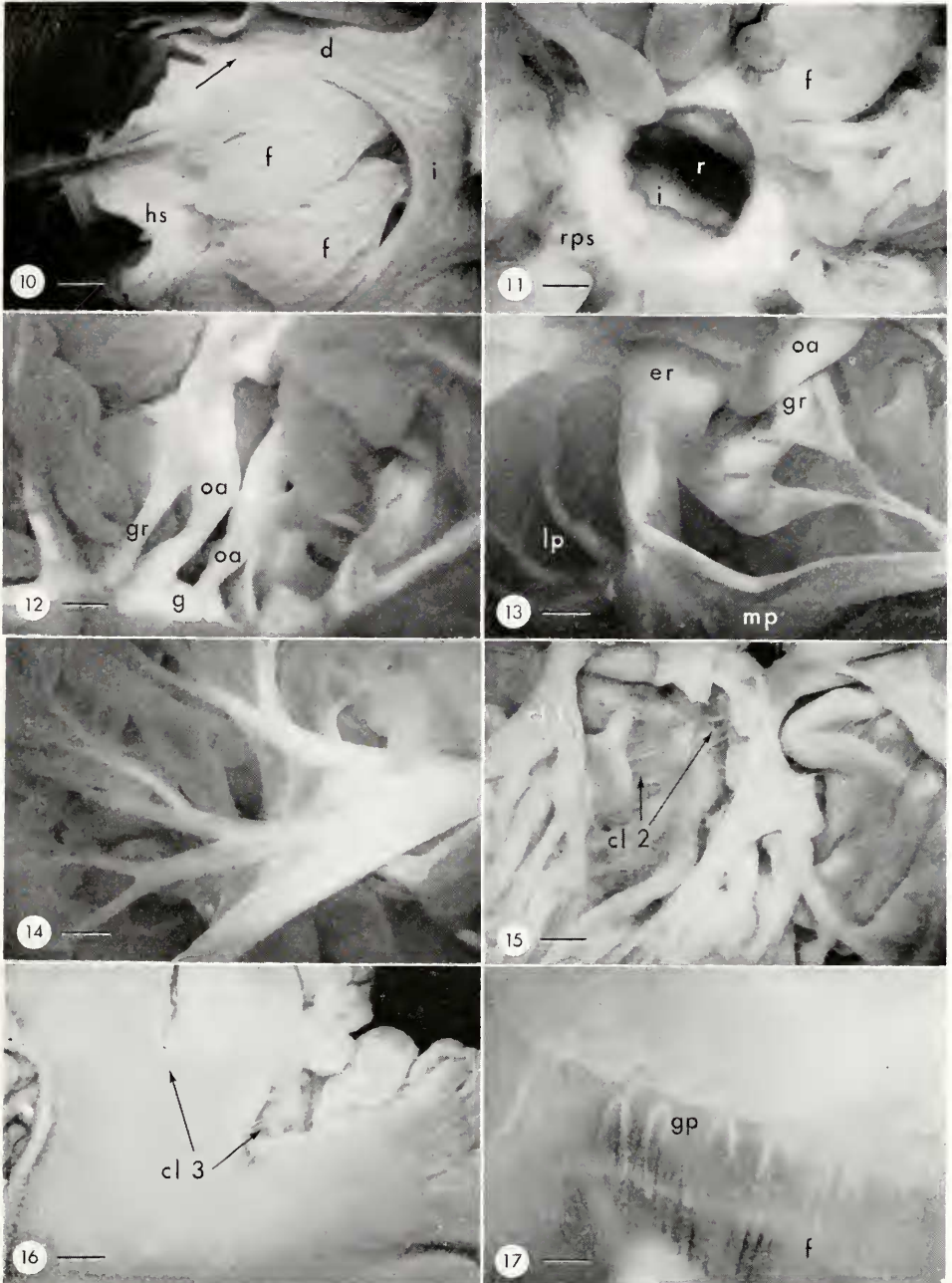


FIGURE 10. Aboral view of a portion of the roof of the pyloric stomach showing its relationship to the intestine and intestinal caeca. Abbreviations are: *i*, intestine; *d*, duct leading to a pair of intestinal caeca, proximal to its point of bifurcation; *f*, fold-pattern; and *hs*, horizontal connective-tissue sheet. The arrow indicates the margin of the duct where the hori-

established, however, without information on their histological characteristics. In *Patiria*, class 2 fibers are muscular, while those designated class 3 appear to consist of thin strands of connective tissue.

DISCUSSION

The distinctive combination of special features presented by the digestive system of *O. reticulatus* suggests that this sea-star is capable of considerable versatility in its feeding habits. The unusually large, extensively eversible cardiac stomach, with its well-developed systems of anchoring and retracting fibers, is structurally and probably functionally similar to that of *Patiria* (Anderson, 1959). It seems primarily adapted for handling large pieces of food outside the body, in the manner characteristic of many carnivorous or omnivorous sea-stars. Observations made in the course of the present study, on specimens maintained in aquaria, confirm that *Orcaster* does envelop food in everted folds of the cardiac stomach. In feeding on a piece of fish, for example, the animal first dilates its mouth; several flattened, somewhat palmate lobes of the stomach (probably the lateral pouches described earlier) protrude in contact with the food and then surround it as they are further

zontal sheet attaches and binds it down to the roof of the stomach. Above the arrow may be seen three of the many strands by which the duct is suspended from the roof of the disc.

FIGURE 11. Central portion of the roof of the pyloric stomach, as viewed from the oral side. Note the coarse folds (*f*) that hang down between the slit-like openings from the paired sets of fold-patterns. Other abbreviations are: *rps*, roof of the pyloric stomach; *r* rectum; and *i*, intestine. The anus opens immediately above the short rectum seen here.

FIGURE 12. Aboral view of a portion of the fibrous girdle (*g*) encircling the upper part of the cardiac stomach, showing two of the ten oral anchors (*oa*) that attach it to the proximal ambulacral ossicles, and a girdle retractor (*gr*) representing part of the extrinsic retractor system (see Fig. 13).

FIGURE 13. One of the paired sets of extrinsic retractor strands in a ray, showing the distribution of its principal branches. Abbreviations are: *er*, the main extrinsic retractor near its origin alongside the ambulacral ridge; *mp*, the branch that inserts principally on the roof of the median pouch of the cardiac stomach; *lp*, the branch that turns laterally under the preceding one and distributes to a lateral pouch of the cardiac stomach (see Fig. 14); and *gr*, a girdle retractor, the third major branch, whose stoutest portion runs directly to the girdle and attaches there. The remaining large strand (*oa*) is one of the oral anchors of the girdle (*cf.* Fig. 12).

FIGURE 14. External view of a portion of one lateral pouch of the cardiac stomach, showing the repeatedly bifurcating class 1 intrinsic retractor fibers distributing in the wall.

FIGURE 15. External view of a portion of a lateral pouch photographed after fixation in Bouin's fluid (to provide enhanced contrast). Some downward-coursing class 1 retractors are shown (*cl 1*), as well as a number of the slender class 2 fibers (*cl 2*) that stretch horizontally between adjacent folds of the stomach wall.

FIGURE 16. The floor of the cardiac stomach viewed from the coelomic side; specimen photographed after fixation in Bouin's fluid. Sets of slender fibers (*cl 3*) are seen running vertically from the gutter-patterns to attach outside the smooth floor of the stomach. These are provisionally identified as class 3 intrinsic retractor fibers.

FIGURE 17. Part of an everted vesicle of the cardiac stomach, seen from its mucosal side, showing part of the array of terminal branches of the gutter-patterns (*gp*) bordering the smooth floor of the stomach (*f*). Through the thin wall of the vesicle may be seen some of the slender, vertical, parallel strands of the supposed class 3 intrinsic retractors, attached to the coelomic side of the stomach wall.

For each figure, the scale bar shown represents 1 mm.

inflated with coelomic fluid. The characteristic branching gutter-patterns, with their associated intrinsic retractor strands, can be clearly seen on the vesicles of the stomach. The animal may remain with its stomach everted for several hours, as the food gradually disintegrates and the products of digestion are transported to the inner parts of the system. In the only published account of the feeding habits of *O. reticulatus* under natural conditions, Thomas (1960) reports having observed a specimen with its stomach everted over a small unattached sponge which appeared to have been partially digested. Thomas also cites an unpublished account by another observer who saw *Orcaster* feeding on a sponge. Further unpublished observations by Dr. Jerald Halpern (communicated to me by letter) confirm the fact that *O. reticulatus* consumes large pieces of detritus. Toponce (1973) reports that the related Eastern Pacific species *O. occidentalis* feeds on clumps of stony coral, or on bits of algae. All available evidence thus substantiates the supposition that might have been made on anatomical grounds alone: that *Orcaster* functions as a macrophagous carnivore or scavenger.

It is evidently capable of other modes of feeding as well. Thomas (1960) writes: "I have observed *Orcaster* many times with its stomach everted into small depressions in the coralline sand and *Thalassia* bottoms on which it lives. Examination reveals nothing either in the depression or in the stomach which might be of food value. Possibly any organic material close to the stomach wall is digested in this manner." Halpern (personal communication) also mentions having observed this type of feeding behavior in *Orcaster*. The phenomenon is interesting in view of the analogous behavior exhibited by *Patiria miniata*, as described by Anderson (1959). This species is very frequently seen in tide pools with its voluminous cardiac stomach fully everted, although no visible objects of food are enfolded by it. In an aquarium, the animal applies its everted stomach to the wall, as though digesting the film of microorganisms adhering to the glass. Anderson (1959) suggested that *Patiria* might be using its everted stomach as a flagellary-mucous feeding organ, to collect suspended particulate matter. Araki (1964) reports that under experimental conditions specimens of *Patiria* with everted stomachs are capable of rapidly removing organic compounds from solution in the surrounding water, and his suggestion is that the stomach is involved in this function. Although there appears to be some question as to the significance of dissolved organic matter in the overall nutrition of marine animals (Jørgensen, 1976), the thin-walled stomach seems ideally suited to mediate whatever exchange of materials may take place between sea water and the enclosed coelomic fluid. All things considered, one may justifiably conclude that whatever *Patiria* is doing with its stomach everted in the absence of visible, macroscopic food, *Orcaster* is probably doing something similar.

Further evidence of versatility in feeding is provided by the presence of highly specialized features in the digestive system above the level of the cardiac stomach. These include the very elaborate Tiedemann's pouches, the highly folded structures in the roof of the pyloric stomach, and the unusually large intestinal caeca. Such features as these are never found in strictly carnivorous sea-stars such as *Asterias* and its relatives; there, the pyloric stomach is small and simple, Tiedemann's pouches are lacking, and the intestinal or rectal caeca are strongly reduced. The

more highly specialized structures are characteristic of forms known to be, or suspected of being, microphagous particle-feeders. In all sea-stars, even carnivores, there is a consistent pattern of flagellary circulation through the digestive system. Tiedemann's pouches are interpreted as flagellary pumping organs, functioning to enhance the volume and velocity of water-flow through the gut in connection with the exploitation of suspended particulate matter as food (Anderson, 1960).

The remarkable anatomical similarity between the Tiedemann's pouches of *O. reticulatus* and those of *Porania* is significant in this regard. As long ago as 1915, Gemmill provided experimental evidence that *Porania* can be maintained without weight-loss for long periods (several months) with no food other than suspended particles. In describing Tiedemann's pouches in *Porania* many years later, Anderson (1961) called attention to their unusually complex structure, involving the development of many subsidiary pouches branching from the main one. The conclusion is unavoidable that this elaboration is related to the demonstrated ability of *Porania* to subsist on particulate food alone. It is of interest that Jangoux (1972) has described similar secondary Tiedemann's pouches in *Archaster angulatus*; they are present also in *Dermasterias imbricata* (Anderson, unpublished observations). It is perhaps not unreasonable to suggest that sea-stars with subsidiary or accessory Tiedemann's pouches are at least facultative particle-feeders.

Species in which Tiedemann's pouches are well developed characteristically possess much larger intestinal caeca than those lacking such structures. *Henricia* and *Patiria* both demonstrate this correlation to a considerable degree (Anderson, 1966), as do their relatives *Echinaster* and *Asterina* (Jangoux and van Impe, 1971). If the supposition is justified that Tiedemann's pouches are significantly related to a capacity for particle-feeding (Anderson, 1960), it is tempting to go one step further and suggest that well-developed intestinal caeca are also involved somehow in this function. Here again, *Porania pulvillus* provides a key example. The intestinal caeca of this species are very large indeed, and Gemmill (1915, p. 12) describes their rhythmic contraction and expansion, "sometimes with such activity as to suggest the systole of the auricular portion of a heart." According to Gemmill, *Porania* periodically inflates its gut with water, which is drawn in through the mouth and later expelled forcefully from the anus. Gemmill believed that the large and muscular intestinal caeca are responsible for the expulsion. Since the caeca lack any intrinsic mechanism for expansion, it seems likely that the pressure required to inflate them with water is provided by the large Tiedemann's pouches, whose centripetal currents converge on the roof of the pyloric stomach and enter the intestine.

The remarkably large, well-developed intestinal caeca of *Oreaster* and of its relative *Culcita* have been referred to earlier, and it will be recalled that Tennent and Keiller (1911) described the intestinal caeca as capable of great distention. They say further (p. 114): "Upon opening some specimens the caeca were found to be greatly distended. Upon stimulation they slowly contracted, the entire organ shrinking to about one-third of its former size. The contents were watery . . ." Although we lack for *Oreaster* any comprehensive series of observations on water-flow through the gut, and on filter-feeding, such as those provided by Gemmill (1915) for *Porania*, the structural similarities between the two forms strongly sug-

gest comparable functions; and direct evidence is not altogether lacking. Halpern, on the basis of unpublished observations, is convinced that *O. reticulatus*, in addition to its other modes of nourishing itself, is indeed a filter-feeder. His letter, previously referred to, states: "In the area I observed it in, it filter-feeds when there is a strong tidal current. There are many loggerhead sponges (*Sphaciospongia vesparia*), and *Oreaster* often uses these as a purchase so as to be able to outstretch one, two, or even three arms. As the current slackens, they abandon this method of feeding. Both the fact of filter-feeding and the current acting as a stimulus have been confirmed (but not conclusively) by some preliminary laboratory experiments."

One further specialization in relation to water-movement in the gut, and possible particle-feeding, is represented by the folded structures in the roof of the pyloric stomach. Abundant wrinkles in this general area are known in a number of sea-stars; Tiedemann (1816) showed something of the kind, with associated vessels, in *Astropecten aurantiacus*, and according to Jangoux, Perpeet, and Cornet (1972) such structures are particularly well-developed in *Asterias rubens*. I know of no other species, however, in which strongly flagellated, radially folded patterns have been described, lying in such an obviously functional, oriented relationship between the radial reservoirs and the opening from the pyloric stomach into the intestine, as they do in *Oreaster reticulatus*. (I am informed by Dr. Michel Jangoux, however, that in an extensive series of unpublished observations on members of the Family Oreasteridae he has found similar structures in *Pentacaster*, *Protoreaster*, and *Culcita*). In a dissected specimen of *Oreaster*, very rapid currents can be demonstrated, using dilute India ink, running through the fold-patterns from the central ducts of the pyloric caeca toward the intestine. In my interpretation, the fold-patterns in the roof of the pyloric stomach, the unusually large intestinal caeca, and the elaborate Tiedemann's pouches form a coordinated set of adaptations which enable *Oreaster* to utilize suspended particulate matter as a source of food. Interestingly, all of these features are present in other members of the Family Oreasteridae (Jangoux, Université Libre de Bruxelles, personal communication).

It is clear, however, from all the evidence, morphological as well as behavioral, that *Oreaster* is not exclusively, or perhaps even primarily, a particle-feeder, as *Henricia* may be (Anderson, 1960; Rasmussen, 1965). It should be borne in mind that even that celebrated, demonstrated particle-feeding species, *Porania pulvillus*, internally so similar to *Oreaster*, does not depend altogether on a particulate diet. Gemmill's statement (1915, p. 14) that "At the Millport Marine Station the *Porania* are never seen feeding on shell-fish, etc., or on their neighbors as other species readily do" seems to imply some such conclusion; but he goes on to say only that "ciliary feeding plays a part in the nutritional economy of *Porania*." Recent studies by Ericsson and Hanssen (1973) have shown that *Porania pulvillus*, in fact, feeds on octocorals, brachiopods, and ascidians, both in its natural habitat and in aquaria.

It is to be hoped that similar studies may soon be made on the feeding biology of *Oreaster reticulatus*, to supplement incidental observations, and to determine the validity of conclusions that can now only be inferred from consideration of the comparative anatomy of the digestive system.

The dissections and observations on which this report is based, together with preliminary histological procedures, were carried out at the Mote Marine Laboratory, Siesta Key, Sarasota, Florida. It is a pleasure to express to the Director of the Laboratory, Dr. Perry W. Gilbert, my appreciation for his gracious hospitality, for excellent facilities generously provided, and for the valuable assistance of members of the staff, particularly Pat Bird and Susi Dudley. I am grateful also to Dr. Jerald Halpern and Dr. Michel Jangoux for providing details of their unpublished observations on *Oreaster* and its relatives.

SUMMARY

This paper presents, with illustrations, a description of the digestive system of *Oreaster reticulatus*, a species for which such anatomical details have hitherto been unavailable. Special features of the digestive system include a large, highly eversible cardiac stomach with a particularly well-developed system of securing and retracting fibers; a highly specialized pyloric stomach giving rise to paired pyloric caeca, each of which is associated with an unusually elaborate Tiedemann's pouch featuring a series of secondary pouches branching off along its length; and a set of very voluminous intestinal caeca. By comparison with other asteroids for which anatomical details and feeding biology are known (especially *Patiria miniata* and *Porania pulvillus*), it is suggested that *O. reticulatus* is equipped for a variety of modes of feeding. The cardiac stomach is well adapted for the digestion of large pieces of food outside the body; it may also function as a flagellary-mucous particle-collector, as the similar organ of *Patiria* is thought to do. The specializations of the upper part of the digestive system are closely similar to corresponding organs in the known particle-feeding species *Porania pulvillus*, and it seems probable that *Oreaster* may use its Tiedemann's pouches and intestinal caeca to bring particle-laden water into the digestive system in a manner similar to that described for *Porania*. Such direct observations as are available on the feeding behavior of *O. reticulatus* tend to confirm the conclusions inferred on indirect, anatomical grounds.

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